Five-year radial growth of red oaks in mixed bottomland hardwood stands

Luben D. Dimov [a,*], Jim L. Chambers [a,1], Brian Roy Lockhart [b,2]

[a] School of Renewable Natural Resources, Louisiana State University Agricultural Center, Baton Rouge, LA, USA
[b] USDA Forest Service, Southern Research Station, Center for Bottomland Hardwoods Research, PO Box 227, Stoneville, MS 38776, USA

Abstract

We studied the relationships among 5-year radial (diameter and basal area) growth of red oak (genus *Quercus*, subgenus *Erythrobalanus*) crop trees and predictor variables representing individual tree vigor, distance-dependant competition measures, and distance-independent competition measures. The red oaks we examined are representative of the commercially and ecologically important oak species of the bottomland hardwood forests of the southeastern US. The crown class score, a quantitative measure of crown class and tree vigor, performed best in accounting for the variability in tree diameter growth. Plot-level variables failed to account for a significant proportion of the variability in tree radial growth. The basal area of the first-order neighbors that were taller than the crop trees and located within 2.4 times the mean overstory crown radius had the highest negative correlation with crop tree 5-year radial growth. Red oaks were a major part of these competitors and likely exerted the greatest competitive pressure. However, crop tree radial growth was positively associated with the basal area of the red oaks which were indirect (second order) neighbors and which were taller than the crop trees. It is possible that indirect neighbors do not compete with the crop trees, but they likely compete with the direct competitors of the crop trees, thus having an indirect positive influence on crop tree growth. Such reasoning is consistent with previously observed spatial dependence up to four times the mean overstory crown radius. The findings may have implications for thinning hardwoods stands and crop tree management in that foresters need to take into account (1) oak intra-genus competition, (2) the negative competitive effect of direct neighbors, and (3) the potentially positive effect of the indirect neighbors, the competitors' competitors. Published by Elsevier B.V.

Keywords: Red oak growth; Inter- and intra-genus competition; Mixed bottomland hardwoods

1. Introduction

Tree competition has been a subject of much interest in forestry research. Independent variables are often employed to represent competition effects that explain growth in diameter, basal area, and other tree growth traits. Some of these variables characterize subject tree vigor and competitiveness through absolute or relative dimensions, while others account for competition exerted on the subject tree by neighboring trees. The variables reflecting potential tree competitiveness are individual tree characteristics, often relative to the neighbors', and include diameter, basal area, height, crown class, projected crown area, crown volume, and portion of the crown exposed to direct sunlight. Measures of tree competition were classified by Munro (1974) and others (Dale et al., 1985; Daniels et al., 1986; Tome and Burkhart, 1989; Biging and Dobbertin, 1992, 1995) into two broad categories: distance-independent and distance-dependent competition measures (or indices). The distance-independent variables represent stand-level or plot-level characteristics, including total basal area, density, and basal area of the trees with a height or diameter above a certain threshold (Belcher et al., 1982; Martin and Ek, 1984; Daniels et al., 1986; Wykoff, 1990; Biging and Dobbertin, 1995; Wimberly and Bare, 1996). Accounting for competition through distance-independent variables is a good choice in monospecific plantations where the trees are uniformly distributed and similar in age, size, and growth. Variables

associated with the individual trees, whose growth is modeled, are sometimes included in the distance-independent category.

Competition measures with higher spatial resolution are used to increase model relevance and improve performance in stands that are heterogeneous in species composition or structure. Competition effects are accounted for by the proximity of a subject tree to competitors and their relative size. Distance-dependent measures range in complexity from simple based on inter-tree distance and size (Aaltonen, 1926; Daniels, 1976; Martin and Ek, 1984; Holmes and Reed, 1991; Biging and Dobbertin, 1992), to complex incorporating elements such as estimates of available growing space for the subject tree, point density indices, and influence zone overlaps between a subject tree and its competitors (Spurr, 1962; Opie, 1968; Hamilton, 1969; Bella, 1971; Hegyi, 1974; Lin, 1974; Miina and Pukkala, 2002). The influence zone is defined as an area where the tree is assumed to obtain or compete for resources (Opie, 1968). Some studies have indicated, however, that the inclusion of inter-tree distance in the measure of competition does not necessarily improve model performance (Lorimer, 1983; Ganzlin and Lorimer, 1983; Martin and Ek, 1984; Biging and Dobbertin, 1992). Nevertheless, in mixed species, multi-strata stands, distance-dependent measures of competition may provide a more accurate estimate of a heterogeneous neighborhood influence on individual tree growth.

One of the difficulties associated with distance-dependent competition measures is identification of potential competitors. Identification relates not only to proximity to the subject trees and their relative dimensions, but also to their species. Kittredge (1988) found that in mixed hardwood stands in New England only the basal area of red oaks (subgenus *Erythrobalanus*) in the overstory located within 10 m of northern red oak (*Quercus rubra* L.) subject trees is negatively correlated with the basal area growth of these subject trees. Taking into account other overstory species actually decreased the observed correlation, suggesting that mainly trees from the red oak group are exerting competitive stress on red oak subject trees. Additionally, understory trees were found to not have a negative effect on basal area growth of overstory oaks, suggesting that moisture and nutrients may not be a limiting factor on these sites and that competition in the rhizosphere is minimal when soil conditions are less limiting.

Many studies investigating tree competition have been restricted to plantations or to even-aged, monospecific stands with relatively homogeneous structure. This may explain why the knowledge of tree locations may be of little value in some competition models. Studies that are exceptions and have explored more heterogeneous stand conditions include studies with northern hardwoods (Lorimer, 1983; Holmes and Reed, 1991; Cole and Lorimer, 1994), mixed conifers (Biging and Dobbertin, 1992), and upland hardwoods (O'Neal et al., 1994). The review of the literature did not, however, reveal similar studies in naturally regenerated southern bottomland hardwood forests. Consideration of spatial relationships and species may be important in modeling growth of individual trees in such forests, because they are complex in structure and represent a highly heterogeneous mixture of species (Smith and Linnartz, 1980; Putnam et al., 1960).

We studied the competitive interactions influencing radial growth of selected crop trees from subgenus *Erythrobalanus* (hereafter referred to as red oaks) in bottomland hardwood stands. We compare the ability of subject tree attributes and neighborhood tree characteristics to account for the observed 5-year crop tree growth in diameter and basal area. A period of 5 years is typical and appropriate for such studies because it is long enough to demonstrate characteristic growth patterns without possible annual interference, but is short enough to avoid violating the assumption for unchanged canopy position of plot trees (Kittredge, 1988).

Previous studies established that species from the red oak subgenus exert more intense competition on northern red oak (*Q. rubra* L.) crop trees in New England than do other associated species (Oliver, 1978b; Hibbs and Bentley, 1984; Kittredge, 1988). Therefore, it has been suggested that in mixed stands early thinning to release the oaks is unnecessary unless they are entirely overtopped.

Our work examines if the findings for northern red oak in New England are also applicable to southern hardwoods, i.e., if red oaks are the major competitors of other oak crop trees in the same strata. Rather than add to the existing array of competition indices or testing their performance, we tried to uncover underlying competitive or mutualistic interactions and associations, especially with consideration to inter-tree distances. Because we do not provide indication of resource levels other than sunlight through crown attributes, some may find it more appropriate to use the term plant interaction in places where we use the term competition.

2. Materials and methods

2.1. Study areas

The study was conducted in relatively undisturbed natural stands in major and minor stream bottomlands in the southern United States. The red oak component criteria for stand selection included the presence of cherrybark oak (*Quercus pagoda* Raf.), the species of main interest, and a visually estimated red oak component of at least 10% by basal area. The stands were assumed to have an even-aged overstory—many mixed species hardwood stands establish after major disturbances and most trees occupy the site within a relatively short period of time (Oliver, 1978a, 1980). Further canopy stratification is usually a result of species-specific height growth patterns and biological limitations, rather than substantial age differences. We selected at least 12 plots that met the search criteria in each stand, recorded their geographic positioning system (GPS) coordinates, and randomly selected three plots per stand. The plots had a red oak crop tree serving as plot center.

We installed three plots in each of four bottomland hardwood stands from a three-state area: one stand in central Louisiana on a major stream bottom (as defined in Meadows and Hodges, 1997) and three stands on minor stream bottoms—

northern Louisiana, southeastern Arkansas, and northeastern Mississippi. The stands were on either clay loam or silt loam soils and had little harvesting (two of the stands) or no harvesting (two of the stands) since establishment. More detailed stand and plot information is available in Dimov et al. (2005).

2.2. Data collection

The square plots were 0.64 ha each. All potential plots had a dominant or codominant cherrybark oak subject tree at the center of the plot. Plots where at least one adjacent tree in the same strata was a red oak were preferred. All plot trees with diameters at breast height (dbh, 1.37 m above ground) > 10.0 cm were flagged and numbered. We recorded dbh, species, tree coordinates on the plot, and crown class. We used the crown classification developed by Kraft (1884) (as cited by Assmann, 1970), and later modified to its present form (Smith et al., 1997). Total tree height and crown radius in the four cardinal directions were collected for all dominant, codominant, and intermediate trees. Two overstory trees that were immediate neighbors of the central tree, as defined by "touching" crowns or in proximity, were selected and later harvested with the central tree for growth measurements. We measured the radius of the vertical crown projection for the central tree and the two selected neighbor trees in eight directions and also determined their numeric crown class score (Meadows et al., 2001). The score is based on: (1) direct sunlight from above – values from 0 to 10; (2) direct sunlight from the sides – 0–10; only the upper half of the crown is used; (3) crown balance – 1–4 according to the number of quadrants occupied by >20% of total crown volume; (4) relative crown size – 1–4 for appropriate crown size and density as related to a tree of that diameter and species. The sum determines the crown class: 24–28 points: dominant; 17–23: codominant; 10–16: intermediate; 2–9: suppressed.

We harvested 36 subject trees, of which 32 trees were red oaks. Their average age was considered an indicator of stand age and was determined from the rings at the base. The 32 oak subject trees were from 3 species: 22 cherrybark oak, 9 water oak (*Q. nigra* L.), and 1 Nuttall oak (*Q. nuttallii* Palmer). For the purposes of this study, species differences among the three oaks (Burns and Honkala, 1990) were not taken into consideration and all were combined for analyses. We cut 4 cm thick cross sections from the base, breast height, and every meter to the top of each harvested tree. We placed the cross sections in plastic bags as soon as they were cut and stored them at a temperature of 5 °C for 2–4 weeks before measurements. We used the sections obtained from breast height to measure the annual radial growth for the previous 5 full years. Diameter growth, ΔD, was calculated as the average 5-year radial growth measured in eight directions multiplied by 2.

We harvested the trees from April through June of 2002 on the sites in central Louisiana, northern Louisiana, and Arkansas and March 2003 in Mississippi. Thus, the 5-year radial growth occurred in growing seasons 1997–2001 on all but the Mississippi site, where it was in 1998–2002.

Since no prior measurements were available, an assumption was made that the data collected for the plot trees, except for the harvested trees initial diameter, represented the initial condition in the stand 5 years ago (including the crown measurements and size of neighbors). It is indeed likely that tree relative dimensions and canopy status change little over a 5-year period and other studies have made similar assumptions (e.g., Holsoe, 1948; Hatch et al., 1975; Kittredge, 1988).

2.3. Analyses

We studied the 5-year growth in diameter (ΔD) and basal area (ΔBA) of the harvested red oak trees. Differences in the results of the two dependent variables are to be expected, as the same diameter growth in two trees with different initial diameters will result in greater basal area growth in the tree with larger initial diameter.

Three classes of predictors were used in the models: individual tree variables (subject tree attributes), distance-independent (or plot level) variables, and distance-dependent variables.

Individual tree variables were initial tree dbh (INIDBH) (dbh 5 years prior to cutting), initial tree basal area (INIBA), total crown class score (CSCORE), sum of the crown class score for direct sunlight from above and from the sides only (DIRSUN), crown diameter, crown projection area, and tree height. If excluding the two crown class criteria, crown balance and relative crown size, does not result in large decrease in variance in ΔD and ΔBA accounted for, then using only direct sunlight from above and from the sides instead of all four crown variables would be justified and save field time.

Distance-independent variables were the plot-level variables basal area of 1) trees with dbh > 10.0 cm, 2) unsuppressed trees, 3) red oak trees, and 4) unsuppressed red oak trees.

Distance-dependent variables included three subclasses. Subclass 1 was $BA_{j,k,m}$ (e.g., $BA_{100\%,\ red\ oaks,\ 15.0\ m}$) – total basal area (BA) of the trees that satisfy conditions j, k, and m, which relate to height, species, and distance, respectively. Subscript j takes values "all hts", i.e., trees of all heights were included in the calculation of neighborhood basal area; values "80%" and "100%", indicating that the neighbor tree height had to be equal to or larger than that percent of subject tree height for the neighbors to be included in the calculation of neighborhood basal area. The choice of trees with heights >80% of the subject tree height, although somewhat subjective, is because such trees are in the same general strata and possibly tall enough to influence the subject tree crown and therefore growth. The k represents species and has values "all species" or "red oak species". Finally, m indicates the radii of circles around the subject tree from 2.0 to 21.5 m in 1.5 m increments. For example, a designation $BA_{100\%,\ red\ oaks,\ 15.0\ m}$ indicates BA of trees that are equal in height or taller than the subject tree, are red oaks, and are within a distance of 15.0 m from the subject tree.

Subclass 2 was $BA_{j,k,p}$—total BA of the trees that satisfy conditions j, k, p, where p represents an annulus (the space between two concentric circles) between X and $(X + \Delta X)$ m

from the subject tree. The radius X ranges from 2.0 to 21.5 m in 1.5 m increments, and ΔX ranges from 1.5 to 19.5 m in 1.5A m increments, where A is an integer from 1 to 13, and $(X + \Delta X)$ does not exceed 21.5 m (Fig. 1). Only 3 radii X are shown as an example in Fig. 1, which yields 3 possible circles and 3 annuli.
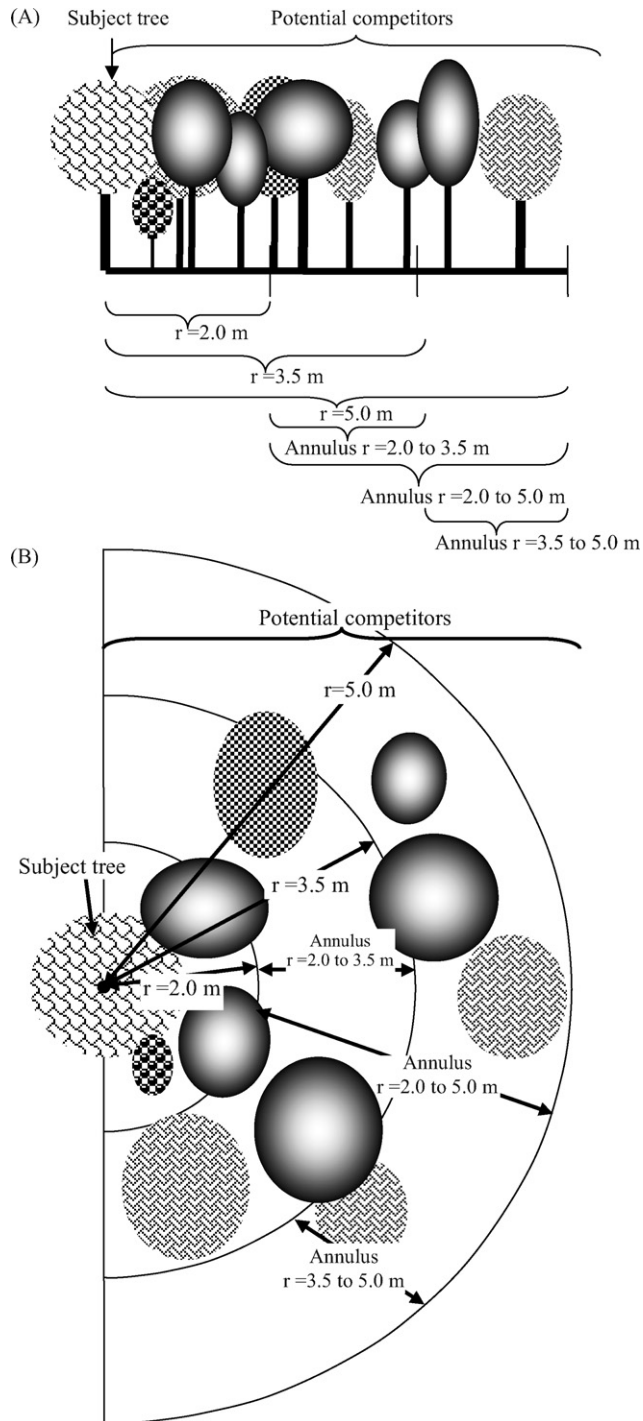

Fig. 1. Semicircle side view (A) and top view (B) representation of the method for determining the BA of potential competing trees within concentric circles with radius r and annuli (concentric bands) centered on the harvested subject tree. The basal area was summed for each circle and annulus starting from the subject tree up to a distance of 21.5 m. Only three intervals are illustrated for simplification. The actual number of intervals was 14, resulting in 14 circles and 91 annuli.

In the calculations for the study there were 14 circles and 91 annuli. A designation $BA_{100\%, \text{ red oaks}, 3.5-15.0 \text{ m}}$ for example, indicates the basal area of the trees that are equal in height or taller than the subject tree, are red oaks, and are between 3.5 and 15.0 m from the subject tree.

Subclass 3 consisted of simple competition indices calculated for the independent variables from subclasses 1 and 2. Their form was similar to competition index 1 in Cole and Lorimer (1994) and was

$$C = \frac{\sum BA}{BA_i} \tag{1}$$

where C is the dimensionless competition index, BA_i the basal area of the subject tree, and $\sum BA$ is the sum of the basal areas of the trees in the circles and annuli as described in subclass 1 and 2, respectively. Inter-tree distance is considered the distance between stump centers and not the distance between adjacent crown edges.

As part of a basic exploratory analysis (simple linear regression (SLR) with ordinary least squares (OLS) estimation), which does not take into account the hierarchical data structure (trees within plots within stands), we examined the performance of each group of predictor variables in relation to their ability to account for the variability in ΔD and ΔBA of the harvested trees. A predictor variable was arbitrarily considered significant if the slope had a P-value <0.05. Because clustering in the data (trees within plots and plots within stands) can introduce an additional source of variability and correlation, which is not accounted for by the OLS models, we used generalized least squares (GLS) estimation with mixed models (Proc MIXED in SAS v.9) that take into account the potential presence of the random effects "plot" and "stand". P-values and parameter estimates were obtained from the GLS models, while the OLS models were only used as an exploratory tool. We considered the results from the exploratory analysis and information-theoretic methods (Burnham and Anderson, 2002) to determine the variables in the final models with multiple predictors. Natural logarithm variable transformations found useful in similar studies (Cole and Lorimer, 1994) were used where appropriate as recommended in the statistical literature (Neter et al., 1996).

3. Results

Stand ages for the central Louisiana, northern Louisiana, Arkansas, and Mississippi stands were 78, 68, 73, and 60 years, respectively. The number of trees with diameters larger than 10.0 cm ranged from 309 to 614 trees/ha, with an average of 476 ± 109 (mean $\pm$ 1 S.D.). Red oaks accounted for 5–43% of the total number of trees per plot and 13–73% of the BA. On average, red oaks represented $22 \pm 12\%$ of the trees, but $42 \pm 20\%$ of the BA, indicating that red oaks were trees with large relative diameters. Plot stocking ranged from 94% to 139% and averaged $118 \pm 12\%$ (Goelz, 1995). Thirty-two of the harvested trees were red oaks with 20 of them classified as dominant, 10 as codominant, and 2 as intermediate. The limited

Table 1
Main statistics for major independent variables

Statistic	BA[a] all spp (m²/ha)	BA all spp, non-suppressed[b] (m²/ha)	BA oaks (m²/ha)	BA oaks, non-suppressed (m²/ha)	Subject tree crown projection (m²)	Subject tree mean crown D (m)	Subject tree height (m)	Crown class score[c]	Direct sunlight from above and sides score[c]
Minimum	24.75	20.20	6.45	5.35	34.05	5.70	21.43	13.00	9.00
Maximum	42.79	34.64	25.17	23.38	286.47	18.62	39.09	28.00	20.00
Mean	31.68	24.96	15.59	14.17	107.51	10.63	32.47	23.09	16.53
S.D.	4.34	3.74	5.90	5.69	53.80	2.61	3.85	3.40	2.57

[a] BA, basal area.
[b] Basal area of trees from the dominant, codominant, and intermediate crown classes.
[c] Calculation of the crown class score and the scores for direct sunlight from above and from the sides are explained in Section 2.

number of intermediate trees and the absence of suppressed trees is a result of our focus on crop trees, which are chosen from upper crown classes. The dbh of the 32 oaks ranged from 28.8 to 66.3 cm. Additional statistics of main independent variables are listed in Table 1.

The CSCORE was the best predictor of ΔD among the individual tree variables. It achieved the smallest modified Akaike's information criterion (AICc) (Akaike, 1974) (205.9, Table 2), followed by DIRSUN and tree height (AICc of 207.9 and 221.6, respectively). The relative performance of the variables in OLS models was equivalent.

All individual tree variables were highly significant predictors of ΔBA (Table 2). INIDBH was the best predictor, as suggested by its lowest AICc (334.6). INIDBH also had the higher correlation with ΔBA.

The use of the plot-level variables was not as successful as the use of individual tree variables in explaining the variation in ΔD and ΔBA. The scatterplots of ΔD and ΔBA versus the distance-independent plot variables revealed no particular patterns and no predictor variable was significant.

In the analyses of distance-dependent variables we used GLS models for determining variable significance and AICc, while we used exploratory OLS models for reporting r^2 and for correlogram construction. In nearly all cases, the variables that were found to be the best according to the GLS models (as per the P-value and AICc) were also the best variables in the OLS estimation. The BA of trees from all species with heights ≥80% of the height of the harvested subject trees in the 2.0–8.0 m annulus (BA$_{80\%, \text{all species}, 2.0–8.0 \text{ m}}$) and the 3.5–8.0 m annulus were significant predictors of ΔD accounting for 16% of the variability in ΔD. For the response variable ΔBA there were no

circles or annuli where BA$_{80\%, \text{all species}}$ was significant. There were six annuli where the variable BA$_{80\%, \text{red oak species}}$ was significant at $\alpha = 0.05$ for ΔD and the annulus with the lowest AICc and highest r^2 was again 2.0–8.0 m. Other annuli with significant BA$_{80\%, \text{red oak species}}$ were 2.0–11.0, 2.0–12.5, 2.0–14.0, and 2.0–15.5 m. There were no circles or annuli where tree BA explained a significant amount of the variability in ΔBA. The distance-dependent variables BA$_{\text{all hts, all species}}$ included the suppressed trees. In this case the annulus accounting for the most variability (20%) in ΔD was from 5.0 to 6.5 m. The BAs in several more annuli were significant predictors, but all were fairly similar in their ability to account for the variability in ΔD (14–19%). For ΔBA, the only annulus where BA$_{\text{all hts, all species}}$ was significant was the 3.5–6.5 m annulus, accounting for 15% of the variance.

BA$_{100\%, \text{all species}}$, the BA of trees that were taller than the subject tree regardless of their species, in the 3.5–11.0 m annulus was better predictor of ΔD than the BA$_{100\%, \text{all species}}$ in any other annulus (lowest P-value and AICc, largest r^2 of 46%) (Fig. 2). Other highly significant annuli with $r^2 > 0.40$ were 2.0–11.0 m ($r^2 = 0.45$), 2.0–8.0 m ($r^2 = 0.43$), and 3.5–8.0 m ($r^2 = 0.42$). The annuli whose BA accounted for the most variability in ΔBA were similar to those for diameter growth. The BA$_{100\%, \text{all species}}$ of the trees at a distance between 2.0 and 11.0 m had the highest coefficient of determination (0.25) with ΔBA.

Using the BA of only the red oak trees taller than the subject trees (BA$_{100\%, \text{red oak species}}$) did not contribute to a better model fit. While the exclusion of the non-oak species reduced the variance accounted for and increased AICc and P values across nearly all annuli, the reduction was marginal (i.e., 5–10 points reduction in r^2).

Table 2
General statistics for individual tree-based variables

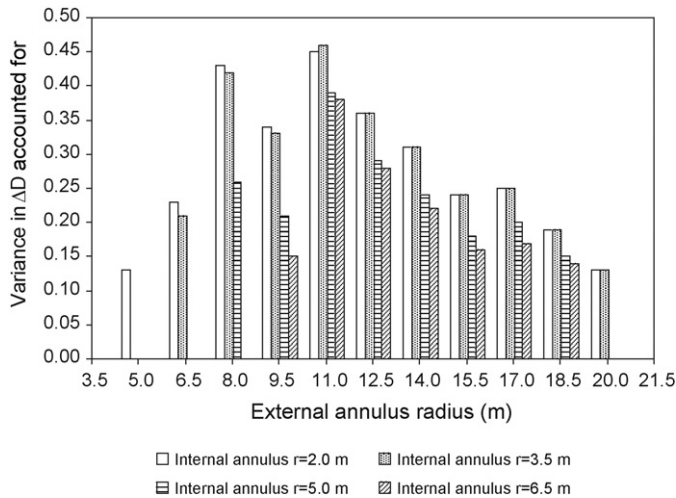| Independent variables	ΔD				ΔBA			
	Intercept	Slope	Slope P-value	AICc	Intercept	Slope	Slope P-value	AICc
Initial tree diameter	16.262	0.229	0.185	226.8	−67.381	5.344	<0.001	334.6
Initial tree basal area	22.777	0.003	0.303	236.0	65.375	0.072	<0.001	346.1
Crown class score	−12.565	1.705	<0.001	205.9	−95.758	11.755	<0.001	337.4
Score for direct sunlight from above and from the sides	−8.258	2.124	<0.001	207.9	−73.760	15.106	<0.001	337.2
Crown diameter	18.830	0.735	0.214	224.5	−5.321	17.127	<0.001	336.4
Crown projection area	22.724	0.037	0.201	230.4	89.370	0.817	<0.001	342.3
Tree height	−3.057	0.919	0.020	221.6	−192.350	11.358	<0.001	336.3

Fig. 2. Coefficients of determination for 5-year diameter growth (ΔD) from simple liner regression models. The independent variables are the basal areas of all trees that are equal in height or taller than the subject tree and located within specific concentric annuli around it.

The competition index C, related to relative BA (Eq. (1)), was calculated for each of the circles and annuli for the five distance-dependent predictor variables ($BA_{80\%, all species}$, $BA_{80\%, red oak species}$, $BA_{all hts, all species}$, $BA_{100\%, all species}$, $BA_{100\%, red oak species}$) and regressed against ΔD and ΔBA. Dividing the summed BA of the competitors by the BA of the subject tree provided better data fit (Table 3) and accounted for more of the variance. OLS regression resulted in coefficients of determination with the competition indices of up to 0.53 for ΔD and 0.49 for ΔBA. Regardless of the independent variable used, the strongest relationships with ΔD and ΔBA were achieved with the BA of the trees located within part of or the entire 2.0–11.0 m annulus (Table 3, Fig. 2).

The increase in BA of the neighbors in the annuli was generally associated with a decrease in ΔD and ΔBA (Fig. 3 shows ΔD, but ΔBA had identical pattern). This was observed for most annuli, but there was an exception with the 14.0–17.0 m annulus (Fig. 4). Closer inspection of the scatterplots of ΔD and ΔBA (Fig. 4 shows ΔBA, but ΔD showed identical pattern) against the BA of the red oaks that were taller than the subject tree showed that when there was no competition present ($BA_{100\%, red oak species, 14.0–17.0 m} = 0$) within this annulus there was a substantial variability in the resulting growth. The exclusion of the data points where $BA_{100\%, red oak species, 14.0–17.0 m} = 0$, however, revealed a relationship for both dependent variables which was not observed for any other annulus. The relationship was such that the parameter estimates of the slopes were positive as the increase in the amount of competition in this annulus corresponded to an increase, rather than a decrease, in both ΔD and ΔBA. After excluding the cases where there were no competitors in the 14.0–17.0 m annulus, the resulting SLR model could account for as much as 30% of the variability in ΔD ($P = 0.06$, $n = 12$) and 41% in ΔBA ($P = 0.02$, $n = 12$). Unfortunately, excluding the observations with no competitors in the studied annulus reduced the number of available data points to just 12. A similar trend, an increase in ΔD and ΔBA with the increase in competition, was observed for $BA_{100\%, all species, 14.0–17.0}$, but in this case the coefficients of determination were not as high: 0.18 for ΔD ($P = 0.11$, $n = 15$) and 0.23 for ΔBA ($P = 0.07$, $n = 15$).

Log-normal variable transformation models resulted in an improved model fit. From the log-transformed tree-based predictor variables, when entered individually as fixed effects in the mixed-effects model, the only significant variables for ΔD were DIRSUN ($P < 0.01$), CSCORE ($P < 0.01$), and subject tree height ($P = 0.02$). The AICc were 6.0, 7.8, and

Table 3
Annuli radii whose BA was the best predictor of the 5-year growth in diameter (ΔD) and basal area (ΔBA)

Independent variable	ΔD			ΔBA		
	Annulus (m)	AICc	Slope P-value	Annulus (m)	AICc	Slope P-value
$BA_{80\%, all species}$	2.0–8.0	234.3	0.025			
	3.5–8.0	234.0	0.024			
$C(BA_{80\%, all species})^a$	2.0–8.0	218.5	0.011	2.0–11.0	331.3	<0.001
	3.5–8.0	218.3	0.011	3.5–11.0	331.1	<0.001
$BA_{80\%, red oak species}$	2.0–8.0	230.5	0.013			
$C(BA_{80\%, red oak species})$	2.0–11.0	212.1	0.001	2.0–11.0	334.8	<0.001
$BA_{all hts, all species}$	5.0–8.0	234.5	0.025	3.5–6.5	361.4	0.057
$C(BA_{all hts, all species})$	5.0–8.0	217.4	0.007	3.5–9.5	330.9	<0.001
				3.5–11.0	331.2	<0.001
$BA_{100\%, all species}$	3.5–11.0	221.1	<0.001	2.0–11.0	355.7	0.002
$C(BA_{100\%, all species})$	3.5–8.0	200.5	<0.001	3.5–11.0	335.4	<0.001
	3.5–11.0	203.1	<0.001			
$BA_{100\%, red oak species}$	2.0–11.0	223.4	<0.001	2.0–8.0	356.4	0.005
				2.0–11.0	355.6	0.002
$C(BA_{100\%, red oak species})$	2.0–11.0	204.6	<0.001	2.0–11.0	335.7	<0.001

The slope of all regression models was negative.

[a] The competition index (C) is calculated by the formula $C = BA_i^{-1} \times (\Sigma BA_{j,k})$, where BA_i is the basal area of the subject tree, and $\Sigma BA_{j,k}$ is the sum of the basal areas of the trees that satisfy conditions j and k, where j indicates the minimum height of the trees relative to the height of the subject tree and has values of either "all hts", 80%, or 100% of the height of the subject tree, and k represents species and takes values "all species" or "red oak species".
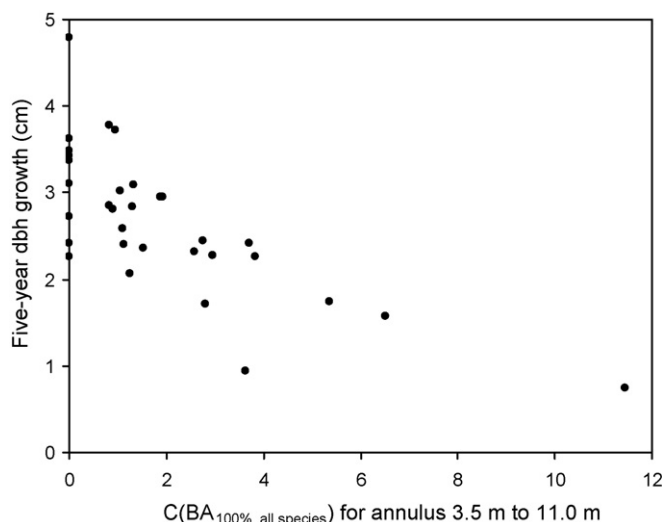
Fig. 3. Plot of 5-year diameter at breast height (dbh, 1.37 m) growth vs. the competition index (C), where C is calculated by the formula: $C = \Sigma BA/BA_i$, where BA_i is the basal area of the subject tree, and ΣBA is the sum of the basal areas of the trees that are taller than the subject tree regardless of their species ($BA_{100\%, \text{all species}}$) and are located in the annulus from 3.5 to 11.0 m away from the subject tree.

83.4, respectively. No combinations of predictors and their interactions could achieve lower AICc and be significant.

The three models for ΔBA with best goodness of fit contained the log-transformed predictors DIRSUN, CSCORE, and subject tree height with AICc of 20.1, 22.3, and 24.0, respectively. Of the mixed models where multiple individual tree-based variables were entered in the model, the model with the lowest AICc (6.5) and significant variables contained the predictors DIRSUN and INIDBH.

For predicting radial growth from individual tree variables we choose the models containing CRSCORE instead of DIRSUN (Table 4), despite their slightly lower AICc, because
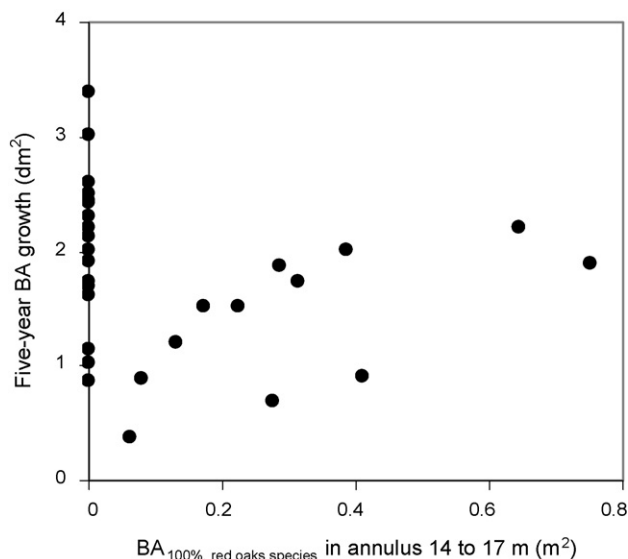

Fig. 4. Scatterplot of the dependent variables 5-year BA growth of the subject trees against the basal area of the red oaks equal in height or taller than the subject tree and located between 14.0 and 17.0 m away.

CRSCORE is a variable that takes into account larger number of important crown traits.

The BA of the non-suppressed trees (log-transformed) was the only plot-level attribute that was a significant predictor ($P = 0.04$; AICc = 42.5) in the mixed models for ΔBA. No other variable or a combination of variables and their interactions were significant in the models for ΔD and ΔBA.

Inclusion of a distance-dependent variable in the models for both, ΔD and ΔBA, resulted in improved model fit, as evident by the decrease in AICc (Table 5).

4. Discussion

4.1. Individual tree variables

Including individual tree variables in crop tree growth models partially addresses concerns that competition, being a growth constraint, not a determinant, has a limited ability to predict crop tree growth (Burton, 1993). Analysis of individual tree variables indicated that factors affecting crown attributes may have the greatest influence on ΔD. While CSCORE was used as an individual tree variable, its value is affected not only by tree characteristics like height, but also by crown position relative to the neighboring trees. Therefore, CSCORE accounts for the amount of above ground competition exerted on the subject tree by immediate neighbors. The CSCORE is fairly fast and convenient to estimate in the field. Simplifying it by estimating only the amount of DIRSUN, i.e., not considering the relative crown size and crown balance (symmetry), resulted in a marginally better fit for both ΔD and ΔBA. However, because crown size and balance reflect tree growth potential (Rock et al., 2004), it is possible that their importance may increase if growth is modeled over a longer period (>5 years). This is partially supported by findings of Holsoe (1948), who found a high correlation (0.93) between the 10-year BA growth and crown diameter of red oaks.

The selected ΔBA model with only individual tree variables included CSCORE and INIDBH as an indication that the two variables complemented each other in accounting for the variability in ΔBA—initial size upon which new BA is formed and the exposure to sunlight (or related factors) may be the primary above-ground factors related to increase in BA growth (Table 4).

4.2. Distance-independent and -dependent variables

None of the plot-level distance-independent variables explained significant proportion of the variability in ΔD or ΔBA, suggesting that in fairly heterogeneous stands local factors and crowding were more important to individual tree growth than were plot-level variables. Although variable transformation suggested that at least the overstory trees may have an impact on ΔBA, the model had a rather high AICc compared to models using individual-tree based variables or distance-dependent variables. In contrast, Wimberly and Bare (1996) found that when they added distance-dependent variables to their model that contained distance-independent

Table 4
Models for 5-year growth in dbh (ΔD) and basal area (ΔBA) with only the individual tree-based predictors

Dependent variable	Independent variable	Parameter estimate	P-value	AICc	Correction factor[a]
ln[b](ΔD)	ln(intercept)	−2.314	0.005	7.8	1.018
	ln(CRSCORE[c])	1.772	<0.001		
ln(ΔBA)	ln(intercept)	−4.599	<0.001	6.9	1.016
	ln(INIDBH[d])	1.217	<0.001		
	ln(CRSCORE)	1.619	<0.001		

[a] Correction factor for bias in log-transformed equations (see Sprugel, 1983 for formulas and background literature).
[b] ln is the natural logarithm.
[c] CRSCORE is the crown class score.
[d] INIDBH is the initial diameter (five full growing seasons prior to cutting).

variables, only a small (<0.01) increase in the adjusted coefficient of multiple determination occurred. In their classification of variables, however, they included INIDBH and crown class in the distance-independent category, while in the current study these variables are classified as individual tree based variables. Similarly, Daniels et al. (1986) found that several distance-independent competition indices based on tree size to mean size ratios, including crown ratio, which they classified as distance-independent measure, performed similarly with the best distance-dependent indices in a loblolly pine (Pinus taeda L.) plantation. In a study of several conifer species, Biging and Dobbertin (1995) were also able to achieve similar model performance with their distance-independent indices that included crown parameters. Although our stand densities varied from 309 to 614 trees/ha and BA from 25 to 43 m²/ha, it is possible that an even greater range in stand densities might have produced plot-level variables that could better account for ΔD and ΔBA.

The crowding of the subject trees, estimated through the distance-dependent variables (BA within concentric circles and annuli around the subject tree), revealed that trees that are equal in height or taller than the subject trees and are located in the annulus from 3.5 to 11.0 m and 2.0 and 11.0 m (for ΔD and ΔBA, respectively) from the subject tree may have the highest negative influence on crop tree 5-year radial growth. When BA of only the red oaks from the same height category and within these same annuli was used as a predictor variable, radial growth model fit decreased marginally. This result might suggests that intra-genus competition from as tall or taller trees may be crucial for crop tree 5-year radial growth. Other studies have found similarly that in mixed upland hardwood stands the canopy red oaks become highly competitive and exhibit strong dominance over other tree species while maintaining low mortality. Oliver (1978a) found that the oaks, while initially inconspicuous, start to dominate the overstory around 40 years after stand establishment. Sometimes the oaks outgrow the other species so much that even-aged stands may have the appearance of uneven-aged (Oliver, 1978b). Because oaks tend to spread their crowns once they are above the general canopy, their major competitors usually become other red oaks (Hibbs, 1981, 1983). Such growth pattern dynamics results in a need for thinning only after the competition becomes intra-specific

Table 5
Models for 5-year growth in dbh (ΔD) and basal area (ΔBA) with predictors considered from all variable types (individual tree based, distance dependent, and distance independent)

Effect	Parameter estimate	P-value	AICc	Correction factor[a]
Dependent variable: ln(ΔD)				
ln(intercept)	0.665	0.594	4.3	1.012
ln(C(BA$_{100\%, \text{ all species, 3.5-11.0 m}}$))[b]	−0.264	0.018		
ln(CSCORE)[c]	0.856	0.035		
Dependent variable: ln(ΔBA)				
ln(intercept)	−1.456	0.290	−0.3	1.006
ln(initial dbh)	1.202	<0.001		
ln(C(BA$_{100\%, \text{ all species, 3.5-11.0 m}}$))	−0.256	0.015		
ln(CSCORE)	0.664	0.073		
Dependent variable: ln(ΔBA), initial DBH excluded				
ln(intercept)	3.084	<0.001	3.7	1.008
ln(C(BA$_{100\%, \text{ all species, 3.5-11.0 m}}$))	−0.450	<0.001		
CPA[d]	0.484	<0.001		

[a] Correction factor for bias in log-transformed equations (see Sprugel, 1983 for formulas and background literature).
[b] C(BA$_{100\%, \text{ all species, 3.5–11.0 m}}$) is the competition index $C = \text{BA}_i^{-1} \times (\Sigma\text{BA}_{100\%, \text{all species}, 3.511.0\,\text{m}})$, where BA$_i$ is the basal area of the subject tree, and $\Sigma\text{BA}_{100\%, \text{all species, 3.5–11.0 m}}$ is the sum of the basal areas of the trees that are at least as tall as the subject tree, are of any species, and are in the annulus between 3.5 and 11.0 m from the subject tree (see Fig. 1 for graphical explanation). Annulus is the space between two concentric circles.
[c] CRSCORE is the crown class score.
[d] CPA is the crown projection area.

(Hibbs and Bentley, 1984), which for northern red oak in New England is reported to be around age 45 years. Kittredge (1988) found that 5-year BA growth of overstory northern red oaks is negatively related to the BA of neighboring oaks with crowns in the same stratum. In some instances, southern red oaks have also been suggested to have similar development patterns. Clatterbuck and Hodges (1988) noted that in mixed cherrybark oak–sweetgum stands in minor river bottoms in Mississippi cherrybark oak tends to overtop the initially faster-growing sweetgum by the age of 20–25 years. Although it can be argued that in our study the oaks appeared to be major competitors because they dominated the overstory, there were many non-oak species that also occupied the top strata, including in the immediate vicinity of the subject trees. Overall, 58% of plot BA was in non-oaks and overall at least 42% of the BA of trees over 80% as tall as the subject trees (in the same strata) and within 8, 9.5, 11, 12.5, 14, and 15.5 m (i.e., in the immediate vicinity) of the subject trees was also in non-oak species.

Larger AICc values and smaller coefficients of determination in the models using the BAs of trees of all heights (i.e., including suppressed trees) compared to models using only overstory trees that are taller than the subject trees, suggests that trees from the lower strata might not be as strong a competitors of the upper stratum red oaks. Therefore, it is likely that the competition for light and other aboveground resources (e.g., physical growing space), rather than for belowground resources, may be critical in the examined bottomland hardwood stands. An observational experiment similarly reported lack of negative relationship between understory presence and growth of overstory trees (mostly northern red oaks) on two adjacent mixed hardwood stands that had not been treated since establishment (Kelty, 1984). In a manipulative experiment involving plots where the understory was actually removed, Kelty et al. (1987) again found absence of negative understory effect on overstory northern red oak growth. Kittredge (1988) also reported that accounting for the amount of understory does not contribute to a better red oak BA growth model in mixed hardwood stands in New England. In areas with lower precipitation, however, the understory does appear to have some impact on overstory growth (Rogers and Brinkman, 1965; Bower and Ferguson, 1968).

A visual comparison of the performance of the distance-dependent variables (Fig. 2) reveals that regardless of which one is used, the most significant variables were the BA of the trees located within either a portion of the 2.0–11.0 m annulus or the whole annulus. The distance of 2.0–11.0 m corresponded to 0.4–2.4 times the quadratic mean crown radius of the unsuppressed trees. Therefore, if a circle with radius 11.0 m (2.4 multiplied by the quadratic mean crown radius of the unsuppressed trees) is drawn around the crop tree, the circle will likely confine all immediate neighbors. This result would have the practical implication that thinning the trees taller than the crop tree within a distance of 2.4 times the crown radius would allow for elimination of the main competition influence at least over the next 5-year period and for free space between the crowns of adjacent trees of at least 0.4 times the mean crown radius. This distance would likely be sufficient for the trees not

to compete severely through mutual shading and crown abrasion and not leave much unoccupied growing space between their crowns. A consideration during any thinning in hardwood stands with some oak component however, should be the possibility of epicormic branching. Creating large openings may result in the proliferation and survival of epicormic branches on the less vigorous trees of susceptible species. Many of the red oaks are indeed susceptible to epicormic branching, including cherrybark and water oak (Meadows, 1995).

Scatterplots of tree BA within nearly all annuli versus ΔD or ΔBA indicated a decrease, whether significant or not, in tree radial growth with an increase in annuli BA. The same was true for the scatterplots where the dependent variables were plotted against the competition index (Eq. (1), Fig. 3). In cases where there were trees present in the 14.0–17.0 m annulus that were equal to or greater in height than the subject tree (12 instances), however, ΔD and ΔBA actually increased with an increase in BA of the trees in this annulus (Fig. 4). Considering the crown radius of the unsuppressed trees averaged 4.5 m, the trees in this annulus are confined at a distance between 3.1 and 3.8 times this mean crown radius. It should also be noted that the BA and crown projection area in these stands were found to exhibit spatial dependence (continuity) up to nearly the same distance of 4 times the crown radius of the overstory trees (Dimov et al., 2005). Trees located between 3.1 and 3.8 times the mean crown radius are located where the crop tree indirect (second order) neighbors would be. Thus, the trees confined in the 14.0–17.0 m annulus may be close enough to compete with the immediate neighbors of a crop tree, but too far to compete with the crop tree itself. Indirect competitors in this distant annulus may therefore have an indirect positive impact on crop tree growth. Such propagation of competitive effects has been reported in other plant species. Harper (1977) summarized a study by Yoda et al. (1957) who reported the presence of a negative correlation between the weights of individual maize (*Zea mays* L.) plants and their first-, third-, and fifth-order neighbors in the crop row, but positive correlation with the weights of the second and forth-order neighbors. Similarly, the positive correlation between the second-order neighbors BA and the growth of the crop tree may be through their negative influence on the immediate neighbors. Trees in our natural stands had a larger number of first, second, third, and higher order neighbors compared to the row crop plants in Yoda et al. (1957). As a result, competitive effects in the forest were likely spread over more first-, second-, and third-order neighbors resulting in a lack of detection of a measurable relationship between the dependant variables and third- and higher order neighbors.

4.3. Models taking into account predictors from all three classes

Although the overall conclusions from the OLS (simple linear regression) and GLS (mixed model) estimation were consistent in their rating of variables, the mixed models more accurately reflect the hierarchical structure of the data and they included a specification of the random effects (plot and stand). The best-mixed models with variables from the three subclasses

generally contained the same predictors that also performed best in the OLS models. The model fit consistently improved as distance dependent variables were introduced in the models for both ΔD and ΔBA, confirming the importance of this class of variables.

The results indicated that 5-year radial growth of selected red oak crop trees in the studied bottomland sites may be significantly negatively influenced by the number of taller competitors located between 0.8 and 2.4 times the mean crown radius, especially by the red oak component. Radial growth may be positively affected however, by the indirect neighbors through their negative influence on the immediate neighbors. The quantitative measure crown class score, crown size, and tree height appear to be reliable predictors of radial growth.

Future work should be directed towards testing through manipulative experiments with removal of trees that are suggested by this study to be the most influential competitors. Particular consideration should be given to the species of the neighbors, their height (relative to the height of the crop tree), and their distance to the subject tree. The positive effect of the indirect neighbors might be tested by removing them and studying the response of the crop trees. Based on indications from a small number of observations in this study, the resulting crop tree growth should be affected negatively by removal of the indirect neighbors.

References

Aaltonen, V.T., 1926. On the space arrangement of trees and root competition. J. Forest. 24, 627–644.

Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Automatic Control 19, 716–723.

Assmann, E., 1970. The Principles of Forest Yield Study—Studies in the Organic Production, Silviculture, Increment and Yield of Forest Stands. Pergamon Press, Oxford, 506 p. (Translation from Assmann, E., 1961. Waldertragskunde. BLV Bayerischer Landwirtschaftsverlag GmbH, München, Federal Republic of Germany).

Belcher, D.W., Holdaway, M.R., Brand, G.J., 1982. A Description of STEMS—The Stand and Tree Evaluation and Modeling System. Gen. Tech. Rep. NC-79, USDA Forest Service, St. Paul, MN, 18 p.

Bella, I.E., 1971. A new competition model for individual trees. Forest Sci. 17, 364–372.

Biging, G.S., Dobbertin, M., 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. Forest Sci. 38, 695–720.

Biging, G.S., Dobbertin, M., 1995. Evaluation of competition indices in individual tree growth models. Forest Sci. 41, 360–377.

Bower, D.R., Ferguson, E.R., 1968. Understory removal improves shortleaf pine growth. J. Forest. 66, 421–422.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, Second ed. Springer-Verlag, New York, USA.

Burns, R.M., Honkala, B.H. (technical coordinators), 1990. Silvics of North America. 2. Hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC, vol. 2, 877 p.

Burton, P.J., 1993. Some limitations to static indices of plant competition. Can. J. Forest Res. 23, 2141–2152.

Clatterbuck, W.K., Hodges, J.D., 1988. Development of cherrybark oak and sweet gum in mixed, even-aged, bottomland stands in central Mississippi, U.S.A. Can. J. Forest Res. 18, 12–18.

Cole, W.G., Lorimer, C.G., 1994. Predicting tree growth from crown variables in managed northern hardwood stands. Forest Ecol. Manage. 67, 159–175.

Dale, V.H., Doyle, T.W., Shugart, H.H., 1985. A comparison of tree growth models. Ecol. Model. 29, 145–169.

Daniels, R.F., 1976. Simple competition indices and their correlation with annual loblolly pine tree growth. Forest Sci. 22, 454–456.

Daniels, R.F., Burkhart, H.E., Clason, T.R., 1986. A comparison of competition measures for predicting growth of loblolly pine trees. Can. J. Forest Res. 16, 1230–1237.

Dimov, L.D., Chambers, J.L., Lockhart, B.R., 2005. Spatial continuity of tree attributes in bottomland hardwood forests in the southeastern USA. Forest Sci. 51, 532–540.

Ganzlin, W.K., Lorimer, C.G., 1983. Tests of Rapid Field Method for Evaluating Competition Around Individual Trees. Res. Note 253. Department of Forestry, University of Wisconsin-Madison, 4 p.

Goelz, J.C.G., 1995. A stocking guide for southern bottomland hardwoods. Southern J. Appl. Forest. 19, 103–104.

Hamilton, G.J., 1969. The dependence of volume increment of individual trees on dominance, crown dimensions, and competition. Forestry 42, 133–144.

Harper, J.L., 1977. The effects of neighbors (pp. 151–347) In: Population Biology of Plants, Academic Press, London, 892 p.

Hatch, C.R., Gerrard, D.J., Tappeiner, J.C., 1975. Exposed crown surface area: a mathematical index of individual tree growth potential. Can. J. Forest Res. 5, 224–228.

Hegyi, F., 1974. A simulation model for managing jack-pine stands. In: Fres, J. (Ed.), Growth Models for Tree and Stand Simulation. Royal College of Forestry, Stockholm, Sweden, pp. 74–90.

Hibbs, D.E., 1981. Development of the forest canopy—a key to silviculture. Northern Logger Tim. Process. 29, 62–78.

Hibbs, D.E., 1983. Forty years of forest succession in central New England. Ecology 64, 1394–1401.

Hibbs, D.E., Bentley, W.R., 1984. A growth model for red oak in New England. Can. J. Forest Res. 14, 250–254.

Holmes, M.J., Reed, D.D., 1991. Competition indices for mixed species northern hardwoods. Forest Sci. 37, 1338–1349.

Holsoe, T. 1948. Crown Development and Basal Area Growth of Red Oak and White Ash. Harvard Forest Paper No. 3, 6 p.

Kelty, M.J., 1984. The Development and Productivity of Hemlock-Hardwood Forests in Southern New England. PhD Dissertation. Yale University, New Haven, CT, 206 p.

Kelty, M.J., Gould Jr., E.M., Twery, M.J., 1987. Effects of understory removal in hardwood stands. Northern J. Appl. Forest. 4, 44–46.

Kittredge Jr., D.B., 1988. The influence of species composition on the growth of individual red oaks in mixed stands in southern New England. Can. J. Forest Res. 18, 1550–1555.

Kraft, G., 1884. Beiträge z. Lehre v. d. Durchforstungen usw. (Hanover) (as cited by Assmann, 1970).

Lin, J.Y., 1974. Stand growth simulation models for Douglas-fir and western hemlock the North-western United States. In: Fries, J. (Ed.), Growth Models for Tree and Stand Simulation. Royal Coll. For., Res. Notes 30, Stockholm, Sweden, pp. 102–118.

Lorimer, C.J., 1983. Tests of age independent competition indices for individual trees in natural hardwood stands. Forest Ecol. Manage. 6, 343–360.

Martin, G.L., Ek, A.R., 1984. A comparison of competition measures and growth models for predicting plantation red pine diameter and height growth. Forest Sci. 30, 731–743.

Meadows, J.S., 1995. Epicormic branches and lumber grade of bottomland oak. In: Lowery, G., Meyer, D. (Eds.), Proceedings of the Twenty-Third Annual Hardwood Symposium: Advances in Hardwood Utilization: Following Profitability from the Woods Through Rough Dimension, May 17–20, 1995, Cashiers, NC, pp. 19–25.

Meadows, J.S., Hodges, J.D., 1997. Silviculture of southern bottomland hardwoods: 25 years of change (pp. 1–16). In: Meyer, D.E. (Ed.), Proceedings of the Twenty-Fifth Annual Hardwood Symposium, 25 Years of Hardwood Silviculture: A Look Back and a Look Ahead. National Hardwood Lumber Association, Memphis, TN, 169 p.

Meadows, J.S., Burkhardt, E.C., Johnson, R.L., Hodges, J.D., 2001. A numerical rating system for crown classes of southern hardwoods. Southern J. Appl. Forest. 25, 154–158.

Miina, J., Pukkala, T., 2002. Application of ecological field theory in distance-dependent growth modeling. Forest Ecol. Manage. 161, 101–107.

Munro, D.D., 1974. Forest growth models—a prognosis. In: Fres, J. (Ed.), Growth Models for Tree and Stand Simulation. Royal College of Forestry, Stockholm, Sweden, pp. 7–21.

Neter, J., Kutner, M.H., Nachtsheim, C.J., Wasserman, W., 1996. Applied Linear Statistical Models. McGraw-Hill, Chicago, 1408 p.

Oliver, C.D., 1978a. Even-aged development of mixed-species stands. J. Forest. 78, 201–203.

Oliver, C.D., 1978b. The Development of Northern Red Oak in Mixed Stands in Central New England, vol. 91. Yale University School of Forestry and Environmental Studies Bulletin, 63 p.

Oliver, C.D., 1980. Even aged development of mixed-species stands. J. Forest. 78, 201–203.

O'Neal, D.D., Houston, A.E., Buckner, E.R., Meadows, J.S., 1994. An index of competition based on relative crown position and size. In: Edwards, M.B. (Ed.), Proceedings of the Eighth Biennial Southern Silvicultural Research Conference. Gen. Tech. Rep. SRS-1. U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, Auburn, AL, pp. 172–175.

Opie, J.E., 1968. Predictability of individual tree growth using various definitions of competing basal area. Forest Sci. 14, 314–323.

Putnam, J.A., Furnival, J.M., McKnight, J.S., 1960. Management and Inventory of Southern Hardwoods, vol. 181. USDA Forest Service Agriculture Handbook, 102 p.

Rock, J., Puettmann, K.J., Gockel, H.A., Schulte, A., 2004. Spatial aspects of the influence of silver birch (*Betula pendula* L.) on growth and quality of young oaks (*Quercus* spp.) in central Germany. Forestry 77, 235–247.

Rogers, N.F., Brinkman, K.A., 1965. Shortleaf Pine in Missouri: Understory Hardwoods Retard Growth. USDA Forest Service Research Paper CS-15, 9 p.

Smith, D.W., Linnartz, N.E., 1980. The southern hardwood region (pp. 145–230). In: Barrett, J.W. (Ed.), Regional Silviculture of the United States. John Willey and Sons, New York, 551 p.

Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1997. The Practice of Silviculture—Applied Forest Ecology, 9th ed. John Wiley & Sons, New York, 537 p.

Sprugel, D.G., 1983. Correcting for bias in log-transformed allometric equations. Ecology 64, 209–210.

Spurr, S.H., 1962. A measure of point density. Forest Sci. 8, 85–96.

Tome, M., Burkhart, H.E., 1989. Distance-dependent competition measures for predicting growth of individual trees. Forest Sci. 35, 816–831.

Wimberly, M.C., Bare, B.B., 1996. Distance-dependent and distance-independent models of Douglas-fir and western hemlock basal area growth following silvicultural treatment. Forest Ecol. Manage. 89, 1–11.

Wykoff, W.R., 1990. A basal area increment model for individual conifers in the northern Rocky Mountains. Forest Sci. 36, 1077–1104.

Yoda, K., Kiara, T., Hozumi, K., 1957. Intraspecific competition among higher plants. IX. Further analysis of the competitive interaction between adjacent individuals. Journal of the Institute of Polytechnics, Osaka City University 8, 161–178 (cited by Harper 1977).